EFFECTS OF TEMPERATURE AND RELATIVE HUMIDITY ON EMBRYOGENESIS IN EGGS OF *MAMESTRA CONFIGURATA* (WALKER) (LEPIDOPTERA: NOCTUIDAE)

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Effects of various combinations of temperature and relative humidity on embryogenesis in eggs of Mamestra configurata *(Walker) were investigated. The following temperature thresholds were determined for some stages of embryogenesis: developmental-hatching, (8.5 C), hatching, (5.0 C), developmental (between 0.0 and 2.0 C) and high temperature developmental-hatching threshold, (30.0 C). Temperature and rate of development curves were derived using three different relative humidities(0, 60 and 98%) and a range of temperatures (8.5–30.0 C). Length of exposure to 35.0 and 5.0 C required to produce mortality of 50% and 95%, was determined for eggs of various ages. The age of eggs exposed to 35.0 C did not appear to influence mortality, but was very important in eggs exposed to 5.0 C. The older the eggs, the longer the exposure required to produce 50% and 95% mortality. The effects of daily exposure to 35.0 C and 5.0 C were studied for eggs of various ages. Older eggs could tolerate longer daily exposure to 35.0 C without high mortality than could younger eggs but, when total length of exposure was determined, there was no significant difference in tolerance between older and younger eggs. Daily exposure to 5.0 C had little effect on mortality but lengthened development.*

The developmental rate and temperature curve for eggs of Mamestra configurata *is J-shaped. Practical application of this curve to field populations will increase the accuracy of larval surveys.*

Nous avons étudié les effets de diverses combinaisons de température et d'humidité relative sur l'embryogénèse des oeufs de Mamestra configurata *Walker. Nous avons déterminé les seuils de température pour quelques stades de l'embryogénèse: la température minimale permettant le développement complete de l'oeuf et son éclosion est 8.5 C, et la température maximale est 30.0 C; la température minimale pour l'éclosion seulement est 5.0 C, la température minimale à laquelle l'embryon se développe (sans éclore) se situe entre 0.0 et 2.0 C. Nous avons étudié le taux de développement en fonction de la température (entre 8.5 et 30.0 C) sous trois conditions d'humidité relative (0, 60 et 98%). Nous avons déterminé, pour des oeufs d'âges divers, les durées d'exposition à 35.0 C et 5.0 C causant 50% et 95% de mortalité. A 35.0 C, l'âge des oeufs ne paraît pas affecter la mortalité, mais à 5.0 C, son effet est important: plus les oeufs sont âgés, plus longue est la période d'exposition requise pour obtenir 50% et 95% de mortalité. Nous avons étudié les effets d'expositions journalières à 35.0 C et à 5.0 C sur des oeufs d'âges divers. Les oeufs plus âgés peuvent tolérer une plus longue exposition journalière à 35.0 C que les jeunes oeufs, sans qu'en résulte une mortalité élevée; mais lorsqu'on considère la durée totale d'exposition, on n'observe aucune différence significative entre la tolérance des oeufs âgés et celle des jeunes oeufs. L'exposition journalière à 5.0 C affecte peu la mortalité, mais prolonge le développement embryonnaire.*

Le taux de développement des oeufs de M. configurata *en fonction de la température suit une courbe en forme de "J". L'application d'une telle courbe aux populations naturelles permettra d'obtenir des estimés plus précis de l'état des populations larvaires.*

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INTRODUCTION

Moths of the species *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae), the Bertha armyworm, occur from Mexico City, Mexico in the south (King, 1928) to Keg River, Alberta in the north (Philip, pers. comm). Within this range, the species is of economic importance only in Western Canada and in the State of Washington.

The species was first cited in the economic entomological literature in 1928 in a paper by King (1928). That paper dealt with external structure of the various lifestages, with some aspects of its life history including geographic range and host plants, (rape was not included), and included descriptions of larval damage on various crop plants. His larval and pupal descriptions are still helpful in separating specimens of *Mamestra configurata* from those of other noctuids causing damage to rape.

In Alberta, the species has one generation per year (Beirne, 1971). Eggs are deposited by the females on leaves of host plants early in July. Larvae feed on these until about three-quarters grown and then chew into the flowers, seed pods, bolls or fruit in August and early September. Larvae pupate in the soil and overwinter, emerging as adults the following June and July.

Embryogenesis in eggs of *Mamestra configurata*, from pre-fertilization to eclosion, has been described by Rempel (1951) who mentioned ovipositional habits of this moth and enlarged upon King's (1928) observations of its eggs. One of the more important observations Rempel made, which had important implications for our research was that fertilization at room temperature (20.0 C – 21.0 C) occurred in the second half hour after oviposition.

The serious outbreaks in 1971 and 1972 of larvae of this species on rape (*Brassica campestris* L. and *Brassica napus* L.) stimulated numerous studies, the results of which are now being published.

The male pheromones of *Mamestra configurata* have been studied by Clearwater (1975a,b) and those of females by Struble *et al.*, (1975). Clearwater (1975c) also described the structure and postembryogenesis of the male pheromone system. Bodnaryk (1978) investigated factors affecting diapause development and survival of pupae and Bailey (1976), the effects of temperature on non-diapause development.

In Western Canada, the importance of *Mamestra configurata* increased in 1971 and 1972, partly because of a large increase in rape acreage. After the first serious outbreak of this insect in 1971, the Alberta Department of Agriculture instituted a series of four annual surveys to determine, first, the areas where densities of *Mamestra configurata* were high and where the potential for economic damage great, and second, to follow the changing distribution of these populations in Alberta each year.

A fall pupal survey was conducted in areas where outbreaks occurred that year, and its results enabled estimates to be made about the initial size of overwintering populations. A second pupal survey was conducted in the spring to ascertain winter mortality of overwintering populations. A third survey,

conducted from mid-May until the end of September, involved the use of black light traps to monitor adult emergence and abundance. Larval surveys were conducted in July in areas where light trap captures were considered high, and first and second instar larval populations were monitored 14–21 days after peak adult activity. Based on results of these surveys, a series of maps were prepared which indicated areas of potential economic damage for that crop year. The most important survey was the final one because this confirmed the presence of the damaging larval stage in the field.

The principal weakness of the final survey is its timing. For it to be effective, it should be conducted at a time when the majority of eggs have hatched, but before the larvae have reached a size where they are causing economic damage. If the survey is conducted too early before most of the eggs have hatched, the population estimate resulting may be too low. If left until too late, it may be impossible to devise and implement control measures before considerable damage has occurred.

There were three principal objectives in undertaking this study: (1) to remove some of the guess-work involved in timing the egg and larval survey by developing temperature curves for embryogenesis which could aid in predicting probable hatching time of eggs in the field, (2) to determine the effects on development and viability of eggs exposed to various periods of unfavourable temperature, and (3) to determine the effect of relative humidity on embryonic development in this insect.

GENERAL METHODS

Handling and collecting eggs

Collecting large numbers of eggs of known age was essential for much of the experimental work. The following procedures were used to facilitate collection and aging of these eggs. All eggs used in the following experiment were obtained from moths reared from field-collected pupae.

Eggs for stock use. – Moths were placed in cages containing four rape plants and subjected to a photoperiod of 16L:8D. Eggs were collected once a day at the end of the dark period by removing leaves containing egg clusters. Often it proved necessary to break the clusters into smaller units. The adhesive which binds the eggs to the leaves was softened with distilled water and individual eggs were removed by gently pushing them with a camel hair brush.

Collecting accurately-timed eggs. – A stock culture of male and female moths was caged in a growth chamber at 20.0 C and approximately 60% RH (for some experiments a culture was maintained at 15.0 C). The moths were fed a 10% honey and water solution from wicked containers, the solution being changed twice a week. Since adults of *Mamestra configurata* generally oviposit at night, we reversed the normal photoperiod so that darkness occurred between 0800 and 1600 hours.

Females prefer a rough substrate for oviposition, but, given no choice, will oviposit on almost any surface. Plastic sandwich wrap was avoided by females, probably because they were unable to find a purchase on it. If the cage is lined with this material, the moths show strong ovipositional preference for paper towellling or other rough textured materials. Paper toweling was chosen as the ovipositional substrate because of its availability and ease of handling. The towelling was folded in such a manner that it was able to stand on its own. It was introduced into the cage approximately one hour after dark and replaced 1 3/4 hours later.

Once the paper towelling was removed, egg clusters were examined at X12 magnification under a binocular microscope and were separated into groups of the desired number of eggs with a razor blade. The strips containing eggs were quickly examined and any damaged eggs were discarded. Each strip was then placed in a clean, 1 mm cap vial, ready to be used in the experiment. The top of each vial was covered with plastic screening, held secure by a rubber band. Any eggs remaining from an egg cluster were placed in a vial marked to indicate their origin and were used to check fertility for that group.

EXPERIMENTS AND RESULTS

Development of eggs

Eggs of *Mamestra configurata* are generally deposited on the underside of leaves of the host plant in a tight, single-layered cluster and are oriented with their anterior, micropylar ends pointed away from the substrate (Rempel, 1951). They are yellowish white when first deposited, but become off-white several hours later. Approximately 24 hours later (at 20.0 C), a band of brown pigment appears around the equator of fertile eggs with additional small patches developing in the micropylar area (Rempel, 1951). Approximately eight hours prior to hatching, the egg turns jet black as the larval head capsule becomes visible through the transparent chorion — a stage referred to as the "black spot stage" by Peterson (1964). A more detailed description of the egg was given by Jones (1977).

Viability and size of field-collected versus laboratory deposited eggs

The main purpose of this experiment was to determine if laboratory rearing and handling techniques influenced egg viability or numbers laid when compared to eggs deposited under field conditions.

Methods. – A laboratory culture of adult moths was maintained in a growth chamber at 20.0 C ± 0.5 C and approximately 60% RH. The photoperiod maintained was 16L:8D, a close approximation of field conditions at the time of the experiment. The moths were provided with potted rape plants for oviposition, these being at approximately the same stage of development as were field sown plants. Ten egg clusters of unknown age were removed at random from the caged culture by removing the leaf with the cluster. Each cluster was then divided carefully into groups of 15 eggs as previously mentioned and these placed in 1 mm cap vials. When less than 15 eggs remained, the remaining group was also placed in a 1 mm cap vial. Eggs from each cluster were kept separate so that mortality and number of eggs could be recorded for each cluster.

Field samples of eggs were studied in a field of rape near Lacombe, Alberta. Ten egg clusters, of unknown age, were located and counted and the leaf with each was encased in a fibre-glass screen having a mesh size of 16 threads per cm to prevent access of predators, parasites and larval escape. These cages were inspected twice daily and the number of hatched larvae recorded for each cage.

Results. – The results of this experiment are recorded in Table 1. Although egg viability (97%) did not differ significantly between the two groups, the average size of the laboratory clusters (146.5) was significantly larger than that of field clusters (80.8). Bailey (1976) reported that females of *Mamestra configurata* reared for ten generations on an artificial diet deposited 40–60 eggs per cluster with viability of eggs ranging from 90–97% at temperatures from 8.0–28.0 C.

Temperature thresholds for embryogenesis

Insect embryogenesis is influenced by many external factors which, acting separately or together, restrict developmental potential. Within the range of each of these factors are points designated as thresholds. Continual exposure of an embryo to the factors beyond these points eventually results in death.

One of the most important and easily studied factors influencing embryogenesis is temperature. Insects, being poikilothermic, are greatly affected by ambient temperature. However, only the egg and the quiescent pupal stage are unable to move to a different microclimate to avoid temperature extremes. For this reason, eggs and non-mobile pupae are superior to other stages for study of temperature thresholds.

Table 1. Comparison of size of egg clusters and viability between laboratory and field collected eggs of *Mamestra configurata*.

Field Collected			Laboratory Collected		
No. of eggs	No. hatched	% hatch	No. of eggs	No. hatched	% hatch
56	53	94.64	130	128	98.46
78	75	96.15	189	186	98.41
86	85	98.84	254	247	97.24
42	38	90.48	127	123	96.85
28	28	100.00	95	94	98.95
187	186	99.46	102	99	97.06
119	118	99.16	79	73	92.96
97	95	97.94	163	159	97.55
63	61	96.82	129	129	100.00
52	50	94.34	197	190	96.45
80.8*	78.9	96.82	146.5*	142.8	97.03

*means significantly different based on T-tests ($P < 0.01$).

The developmental threshold. – The developmental threshold is the temperature at which, on the descending scale, development definitely ceases, and at which, on the ascending scale, development begins (Pearis, 1927). Knowledge of this threshold is vital if one is attempting to predict development on the basis of temperature. An experiment was conducted to determine this threshold for embryos of *Mamestra configurata*. Histological studies were made simultaneously.

Methods. Eggs used in this experiment were collected from clusters of over 100 deposited by females maintained at 15 ± 0.5 C. Eggs were placed at experimental temperatures of 0 ± 0.5 C, 2 ± 0.5 C and 4 ± 0.5 C when less than 30 minutes old, thus ensuring (based on Rempel's 1951 paper) that no prior development had occurred.

Two separate clusters of eggs were placed at each temperature. The eggs from each cluster were divided into 20 groups of five eggs each, each group of five being placed in a separate 1 mm cap vial (the eggs of the two clusters were kept separate). All but two vials were placed on a platform in a 160 mm desiccator containing a saturated salt (KNO_3) solution (Winston and Bates, 1960) to maintain the humidity at about 96%. Eggs in one of the remaining vials were fixed immediately in hot, alcoholic Bouins solution while the other vial was removed and placed at room temperature to determine if all its contained eggs were fertile.

Hot alcoholic Bouins was poured into one vial from each group daily for the first five days. After that time eggs were fixed at five day intervals. Standard histological techniques were used to prepare the eggs for staining with Delafield's Haematoxylin and Mallory's Triple Stain (Humason, 1972).

The experiment was concluded when histological signs of development were found in two or more eggs from both vials.

Results. The temperature developmental threshold for embryogenesis of *Mamestra configurata* is between 0.0 and 2.0 C.

Eggs at 4.0 C showed recognizable development after ten days and at 2.0 C after 15 days. No sign of development occurred at 0.0 C even after 40 days (data from eggs kept after end of experiment).

The hatching threshold. – The hatching threshold is the lowest temperature at which hatching of a fully developed larva can occur (Johnson, 1940).

The egg of *Mamestra configurata* is an excellent subject for this type of experiment because darkening of the head capsule always indicates that development is complete and that hatching is soon to follow.

Methods. Three egg clusters, less than one day old, and each containing in excess of 150 individuals, were collected over a period of two days from the stock culture. Each cluster was divided into groups of 50. Surplus eggs from each cluster were placed in 1 mm cap vials and labelled according to their cluster of origin. These eggs were used as spares to be substituted for any infertile eggs in the experimental group. Each of these nine groups of 50 eggs was placed in a 4 mm glass cap vial and labelled so that groups from individual clusters could be identified. All vials were then placed on a platform, at 20.0 C in a 160 mm desiccator which had been partially filled with distilled water to raise the humidity to greater than 90%.

The eggs were observed closely and were allowed to develop to the black head capsule stage. Then, to prevent larval escape, the tops of the vials were covered with a piece of plastic screening, secured by a rubber band. One vial from each egg cluster was then quickly transferred to identical, water-filled desiccators located in incubators set at temperatures of 7.5 ± 0.5 C, 5.0 ± 0.05 C and 2.5 ± 0.5 C. Eggs were observed twice daily and total number of hatched eggs recorded. The eggs were maintained at the experimental temperature for a maximum of 30 days after which they were returned to 20.0 C to determine if the remaining eggs would hatch.

Results. The results of this experiment are summarized in Table 2. The first group of eggs to hatch were those at 7.5 C. The lowest experimental temperature at which eggs hatched was 5.0 C. No eggs hatched at 2.5 C even after 30 days and these failed to hatch even after being returned to 20 C. Examination of these eggs showed that the embryos had died and dried up. There was a greater percentage hatch at 7.5 C (92.2%) than at 5.0 C (66.0%).

Table 2. The hatching threshold for eggs of *Mamestra configurata*.

	Temperature ° C								
	2.5			5.0			7.5		
Replicate Number	1	2	3	1	2	3	1	2	3
Number hatching per replicate of 50	0	0	0	31	33	35	47	44	48
Average percent hatching	0.0			66.0			92.2		

The developmental-hatching threshold. – The developmental-hatching threshold is the lowest temperature at which complete development from fertilization to eclosion can occur (Johnson, 1940). This threshold is the most important of those so far discussed, because, for eggs of some species, it can be used as an aid in determining distribution. Obviously, areas in which the daily high temperature is always below this threshold for a particular insect, will not have that insect present.

This experiment was designed to determine the lowest temperature at which complete development of eggs of *Mamestra configurata* could occur. Three different relative humidities were used to show if

humidity had any influence on development. Previous research had shown that complete embryogenesis could occur at 10.0 C but not at 5.0 C.

Methods. Eggs were collected over a period of three days from a culture of adults maintained at 15.0 ± 0.5 C and 60% RH. The methods used for collecting and handling eggs were identical to those described previously, with the exception that they were collected when less than 1 hour old to insure that little, if any, development had occurred.

For each daily collection, the eggs were divided into ten groups of 30, each group being placed in a 1 mm cap vial. One of the groups was placed at 20.0 ± 0.5 C and left for the remainder of the experiment as a test of egg viability. The remaining nine groups formed the first of three replicates. Each of the nine vials was placed under a different experimental condition. Vials were placed at temperatures of 6.5 ± 0.25 C, 7.5 ± 0.25 C, and 8.5 ± 0.5 C and at relative humidities of about 0%, 60% and 98% for each temperature. Temperatures were maintained in an incubator (6.5 C), in a refrigerated water bath (7.5 C) and in a growth chamber (8.5 C). Relative humidity was controlled in 6 mm cap vials using saturated salt solutions (P_2O_5 for 0%, $Na_2Cr_2O_7$: H_2O for 60% and K_2SO_4 for 98%) (Winston and Bates, 1960).

Eggs were observed daily for sign of development. When embryos reached the black head capsule stage, observations were made every two hours.

Results. Percentage hatch for each control was 90% or greater. In the experimental groups, hatching occurred only at 8.5 C and 98% RH. Development to the black head capsule stage occurred in some individuals at 8.5 C and 60% RH and at 7.5 C and 98% RH. Dissection of a portion of these embryos several days later revealed no outward sign of structural disorder.

The high temperature developmental-hatching threshold. – *Mamestra configurata* has a reported geographic range that spans vastly different climatic regions extending from Keg River in northern Alberta (Philip, pers. obs.) to Mexico City, Mexico (King, 1928). Populations occurring in central and northern Alberta are exposed to cool springs, warm short summers, and long cold winters, their eggs experiencing temperatures ranging from 5.0 C to just above 30.0 C. However, in the southern part of its range, it is likely that eggs of *Mamestra configurata* are exposed to a much higher range of temperatures.

The purpose of this experiment was to determine the high temperature developmental-hatching threshold for eggs of *Mamestra configurata* and to find out whether eggs of the cold adapted populations of Alberta retain some resistance to high temperature (30 C and above).

Methods. This experiment was performed essentially like the previous ones, (developmental-hatching threshold) except that temperatures of 30.0 ± 0.5 C, 31.5 ± 0.5 C, 32.5 ± 0.5 C and 33.5 ± 0.5 C were used. Temperatures of 30.0 C and 35.5 C were maintained in a heated water bath and of 31.5 C and 32.5 C in incubators. Humidities were maintained using saturated salt solutions of P_2O_5 for 0% RH, NH_4NO_3 for approximately 60% RH and $K_2Cr_2O_7$ for 98% RH (Winston and Bates, 1960).

Results. The results of this experiment are summarized in Table 3. The listings are the totals of three replicates of 30 eggs. Unlike eggs in the previous experiment, relative humidity did not have a significant effect on hatching. Of the four temperatures tested, hatching occurred only at 30.0 C regardless of humidity. Some development occurred in eggs at all other experimental temperatures. All eggs (with the exception of some, probably infertile) developed the characteristic brown pigment of the equator and micropylar areas.

Eggs at 32.5 C developed to the point where larvae were clearly visible through the chorion, however, sclerotization and pigment deposition did not occur.

Table 3. High temperature developmental threshold of eggs of *Mamestra configurata* and effects on it by relative humidity.

Temperature in ° C	No. hatching (maximum 90)* 0% RH	60% RH	98% RH
30	84	82	84
31.5	0	0	0
32.5	0	0	0
33.5	0	0	0

*Figures = totals of three replicates of 30 eggs.

Effects of constant temperature and relative humidity on embryogenesis

Effects of exposure to constant temperature and relative humidities of 0%, 60% and 98% on developmental rate. – When dealing with an insect pest species, knowledge of the effects of climatic factors, particularly those of temperature on various stages of its life cycle is imperative if reliable predictions of outbreaks are to be made and if successful control procedures are to be implemented. The most accurate way of determining individual effects of various field conditions on a particular instar of an insect is to duplicate every possible combination of those conditions in the laboratory. This, however, is usually impossible to do or is too time consuming. The usual alternative (although it lacks the same degree of accuracy) is to use a range of constant temperatures, encompassing the range found in nature and to extrapolate from these results to development in the field.

Few authors have attempted to evaluate the effects of relative humidity acting in conjunction with constant temperatures on insect embryogenesis. This is rather surprising when one considers the effect relative humidity can have on development (Buxton, 1932; Ludwick, 1945; and Bursell, 1974). Since *Mamestra configurata* has a large geographic range (King, 1928), it is probably exposed to a considerable range of relative humidities. This experiment was conducted to determine the effects that relative humidity might have on embryogenesis under constant temperature conditions.

Methods. Ten different temperatures combined with three different relative humidities were used to determine the effect of temperature and relative humidity on embryogenesis. The lowest temperature used was 8.5 C (ie., the developmental-hatching threshold); the highest 30.0 C (ie., the high temperature developmental threshold). The remaining temperatures began at 10.0 C and increased at 2.5 C increments. Growth chambers were used to maintain the temperatures of 8.5 C, 12.5 C, 20.0 C, and 25.0 C, and incubators for the remainder. The temperature in each incubator was monitored and found to vary no more than ± 0.5 C when the door was closed. For most experiments, the doors were opened briefly, once a day, to check egg development. Temperatures returned to equilibrium in less than 30 minutes after the door was closed.

Dry P_2O_5 was used to provide 0% RH, and KNO_3 to provide 98% RH at all temperatures used. $NaBr:2H_2O$ was used to approximate 60% RH for temperatures of 10.0 C, 12.5 C, 15.0 C, 17.5 C and 20.0 C, $Na_2Cr_2O_7:H_2O$ for a temperature of 8.5 C and NH_4NO_3 for the remainder (Winston and Bates, 1960). The saturated salt solutions were prepared and placed at the desired temperature 30 days prior to being used to allow them to equilibrate. Humidities in the chambers were checked prior to, during and after the experiment and were always found to be within 6% of the desired humidity.

Eggs used in this experiment were collected as previously described from a culture of adults kept at 20.0 ± 0.5 C and 60% RH. Thirty eggs were placed in each vial. These vials were exposed to the

experimental conditions within one hour of collection. The experiment was replicated three times. Early in the experiment, it became apparent that insufficient numbers of eggs could be collected at any one time to complete a replicate for the temperature treatments. Instead, the eggs of each collection were used in replicating the three relative humidity treatments used at each temperature.

The eggs were examined once a day until they had reached the black head capsule stage at which time observations were recorded at two hour intervals until hatching was complete.

Results. Results of these experiments are summarized in Table 4 and Figures 1–3. Hatching occurred at all temperatures tested. Rate of development (the reciprocal of the total development time measured in hours) showed a strong positive correlation with temperature (correlation coefficients of 0.978, 0.989 and 0.982 were recorded for 0%, 60%, and 98% RH respectively). The fastest development occurred at 30.0 C- the slowest at 8.5 C.

Humidity had considerable effect on development. Development but no hatching occurred at 0% RH for temperatures of 12.5 C and lower, and at 8.5 C for 60% RH. Hatching always occurred first in those eggs at 98% RH followed by those at 60% RH and 0% RH.

Figures 1 to 3 demonstrate the effects of relative humidity and temperature on development. The straight lines (B) are drawn on the basis of the linear regression equation $Y=7.43 + 1{,}966.44x$; $Y=8.15 + 1{,}761.23x$ and $Y=8.22 + 1{,}708.85x$ for 0%, 60% and 98% RH respectively. These lines are the velocity lines and represent the percentage of total development that occurs during one hour at that temperature. The points on and around these lines are the calculated values based on the reciprocal of the mean development time (listed in Table 4).

The hyperbolic curve (A) is based on the mean development time in hours at the experimental temperatures and humidities indicated. The squares on the graph represent the mean development time in hours for that temperature and humidity.

Effects of constant exposure to a temperature of 35.0 C on development of eggs of different ages. –

Results of preliminary experiments had suggested that *Mamestra configurata* is imperfectly adapted to the climatic regime found in the prairie provinces (Putnam, 1972). To perfectly adapt to this climate, the pupal population of *Mamestra configurata* should have an obligatory diapause (diapause development in this insect has been studied by Bailey (1976) and Bodnaryk (1978)). This however, does not always happen since flights of newly-emerged adults have been taken in blacklight traps in late fall, and some field-collected pupae have been shown to develop without exposure to cold (Philip, pers. comm.). These observations suggest that at least part of the population has either a facultative diapause or lacks it completely. The existence of this partial late second generation in the prairie provinces suggests that *Mamestra configurata* may be bi- or multivoltine in more southerly parts of its range.

The main purposes of this experiment were to determine if eggs of *Mamestra configurata* demonstrate a tolerance to high temperature and to discover the length of exposure required to produce 50 and 95% mortality. A temperature of 35.0 C was chosen for two reasons; because previous experiments had shown that this was above the upper developmental-hatching threshold and because temperaures of 35.0 C or greater for periods over 16 hours per day have been recorded in Arizona cotton fields by Fry and Surber (1971), well within *Mamestra configurata*'s range. Their study of the effects of high temperature on embryonic mortality included eggs of *Estigmene acrea*, a species often found in conjunction with *Mamestra configurata*, and which has a similar life cycle in Alberta (Beirne, 1971).

Methods. Eggs used in this experiment were collected from a culture of adults reared at 20.0 ± 0.5 C, as previously described.

Eggs of four different ages (3 hours, 24 hours, 48 hours, and 96 hours) were exposed to 35.0 C continuously for periods of 13, 20, 30, 45 and 67.5 hours. Six replicates of 20 eggs were used for each of the four different ages.

Table 4. Effect of temperature and three relative humidities on mean development time and development rate of eggs of *Mamestra configurata*.

Temperature °C	Mean development time in hours	Mean % development per hour
	0% RH**	
8.5	x	x
10.0	x	x
12.5	x	x
15.0	259.70	0.00385
17.5	226.49	0.00441
20.0	143.28	0.00698
22.5	124.98	0.00800
25.0	108.13	0.00923
27.5	91.70	0.01090
30.0	87.97	0.01140
	60% RH**	
8.5	x	x
10.0	576.19	0.00173
12.5	462.65	0.00216
15.0	252.32	0.00396
17.5	220.71	0.00453
20.0	135.14	0.00740
22.5	118.80	0.00842
25.0	100.92	0.00991
27.5	83.05	0.01200
30.0	78.71	0.01270
	98% RH**	
8.5	879.70	0.00114
10.0	564.59	0.00177
12.5	458.39	0.00218
15.0	250.04	0.00399
17.5	218.88	0.00457
20.0	133.02	0.00752
22.5	116.75	0.00856
25.0	98.60	0.01010
27.5	81.13	0.01230
30.0	76.86	0.01300

(x – did not complete development to eclosion)
(** means of 3 replicates of 30 eggs per replicate)

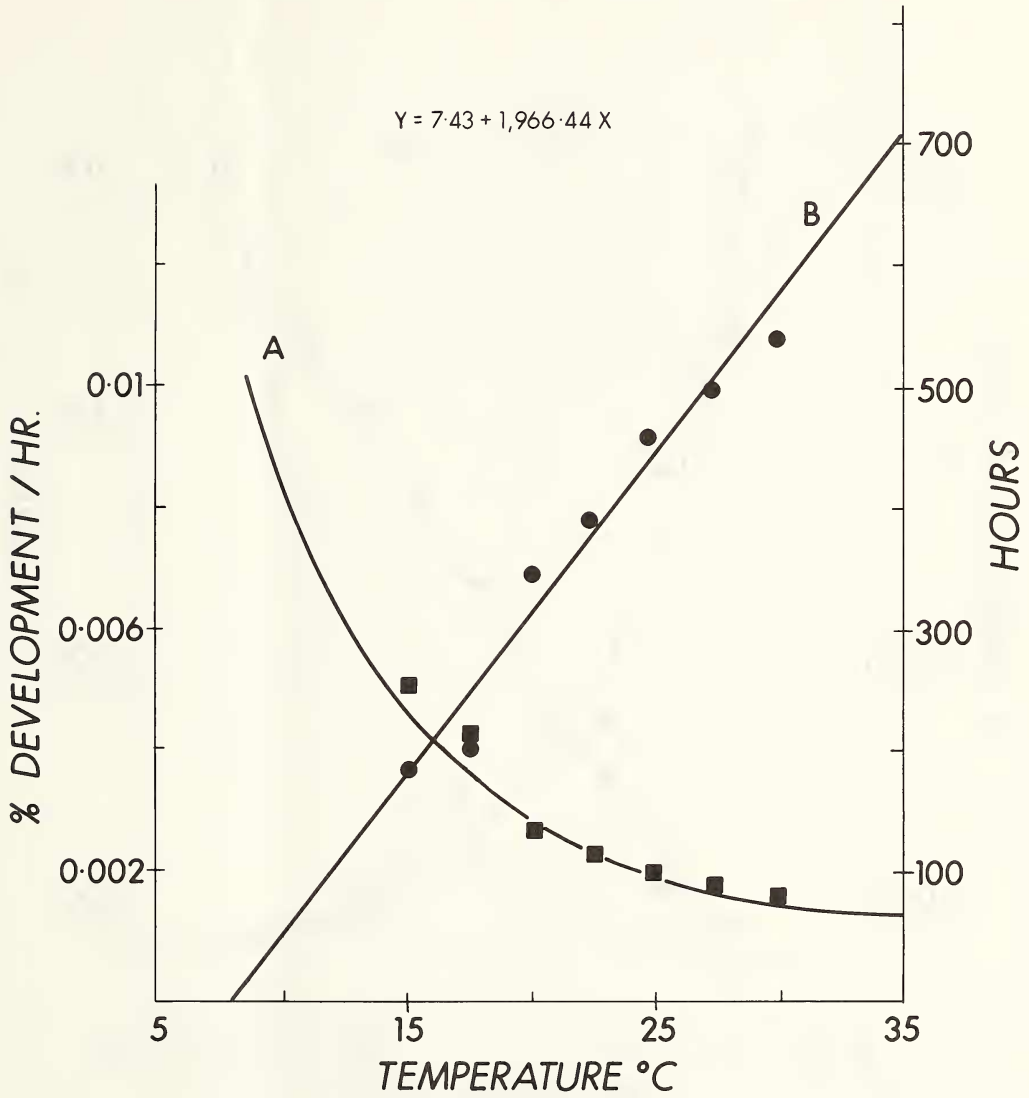

Figure 1. The developmental curve –A; and the velocity line–B; at 0% RH for embryogenesis of eggs of *Mamestra configurata*.

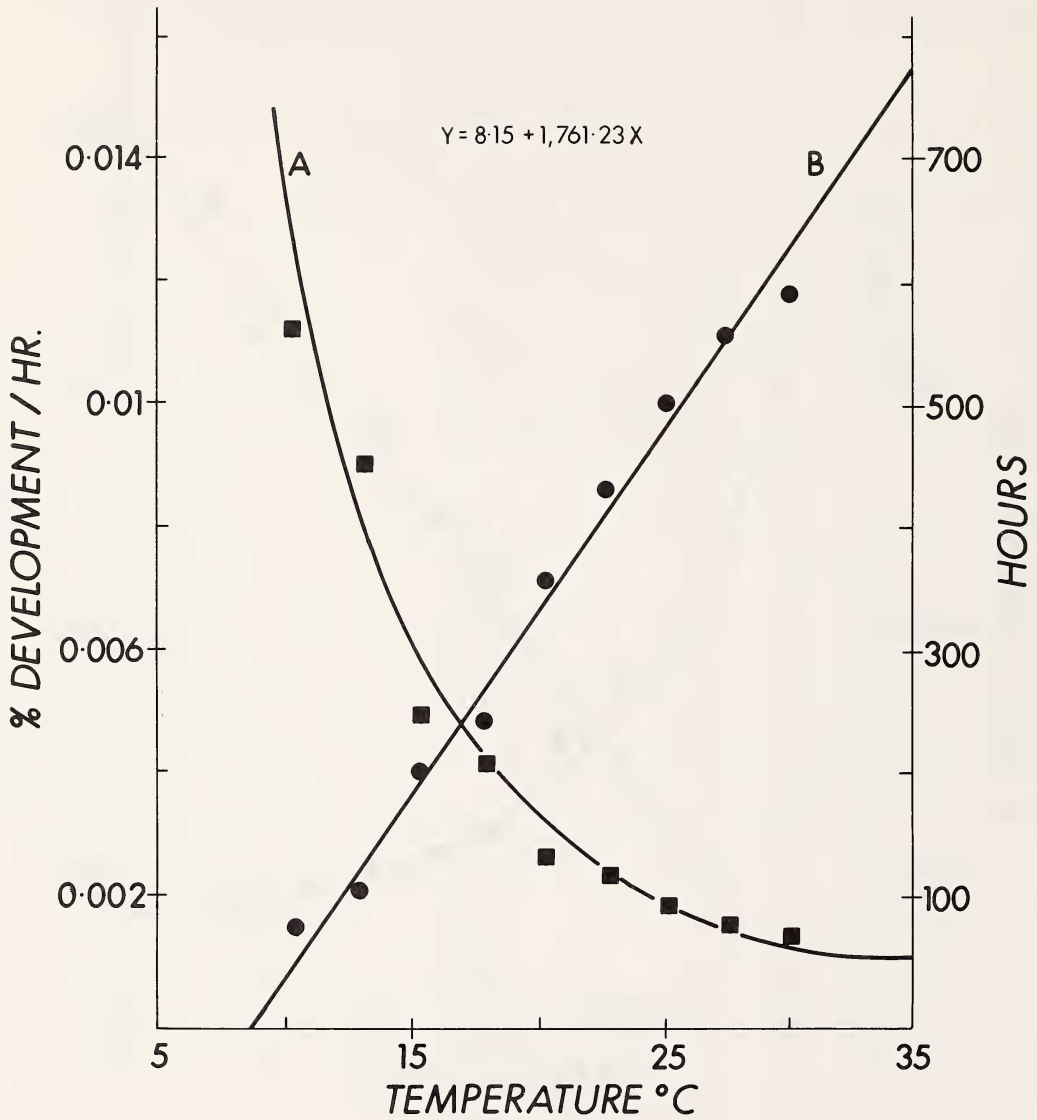

Figure 2. The developmental curve–A; and the velocity line–B; at 60% RH for embryogenesis of *Mamestra configurata*.

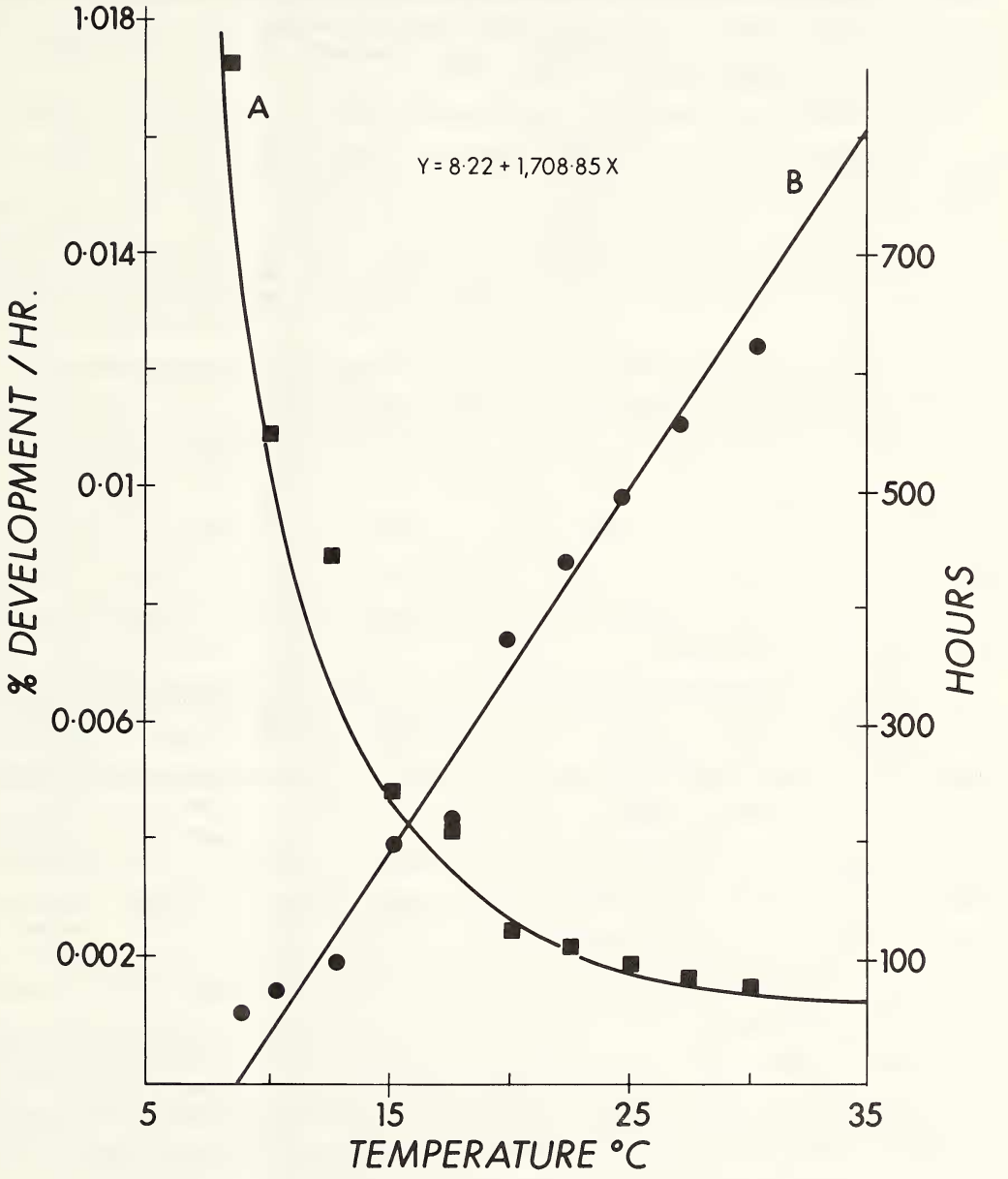

Figure 3. The developmental curve–A; and the velocity line–B; at 98% RH for embryogenesis of eggs of *Mamestra configurata*.

The eggs were collected daily when less than two hours old, divided into groups of six to form replicates, and the remaining vials were used as a check to determine natural mortality. Eggs that were to be used later were left at 20.0 ± 0.5 C and approximately 60% RH until they reached the desired age. When this occurred the eggs were placed in a 160 mm desiccator located in an incubator set at 35.0 C. The humidity in the desiccator was maintained at approximately 60% with a saturated salt solution of NH_4NO_3 (Winston and Bates, 1960).

The temperature in the incubator never varied more than 0.5 C. The temperature in the desiccator and within the vials was checked periodically and showed little variance (0.25 C) from that of the incubator. The incubator was opened only when it was necessary to place or remove vials.

Once the treatment was completed, the eggs in the vials were returned to 20.0 ± 0.5 C and 60% RH, and the tops of the vials were covered with plastic screening to prevent larval escape. The numbers hatching were recorded twice daily. Abbot's formula (Abbot, 1925) was used to determine the net percent mortality. Natural mortality was considered to be the highest mortality that was not a function of the treatment.

Variance analysis was used to determine the amount of variance caused by replication and error.

Results. The results of this experiment are summarized in Tables 5 to 8.

The mean time in hours required to produce 50% mortality were 34.45 ± 1.4, 33.19 ± 3.49, 32.8 ± 1.33 and 35.17 ± 1.11 for 3 hour, 24 hour, 48 hour and 96 hour old eggs respectively; and to produce 95% mortality were 51.27 ± 3.55, 48.31 ± 3.34, 50.03 ± 3.4 and 54.95 ± 4.14 for 3 hour, 24 hour, 48 hour and 96 hour old eggs respectively. From this data it can be concluded that exposures of greater than 37 hours to a temperature of 35.0 C will result in 50% or greater mortality and exposures of 60 hours will result in 95% or greater mortality, to eggs of *Mamestra configurata* regardless of their age.

Variance analysis and the resulting F-values showed that length of exposure was highly significant in deterining mortality (Tables 5 to 8).

Effects of constant exposure to a temperature of 5.0 C on development of eggs of different ages. – When we began this research, we found that *Mamestra configurata* was difficult to rear continuously in the laboratory. Part of the problem was feeding the large number of larvae produced. The main purpose of this experiment was to determine the length of time eggs of *Mamestra configurata* could be stored at 5.0 C without causing excessive mortality. The temperature of 5.0 C was chosen for two reasons: (1) under natural conditions, eggs could be exposed to this temperature or lower (Average minimum temperature for July in rape growing areas in Central Alberta are: Stettler 10.2 C, Vermilion 9.6 C, Edmonton 9.1 C and Calgary 9.5 C (Philip, in note to Heming). Therefore, it is doubtful whether eggs would be exposed very long to temperatures of 5.0 C), and (2) 5.0 C is below the developmental-hatching threshold (8.5 C), but above the developmental threshold (between 0.0 and 2.0 C). A by-product of this research was to determine the length of exposure to 5.0 C required to produce 50% and 95% mortality.

Methods. Procedures used in this experiment were identical to those of the experiment with a constant temperature of 35.0 C , with the following exceptions: (1) the exposure was to 5 C; (2) $NaBr.2H_2O$ (Winston and Bates, 1960) was used to maintain approximately 60% RH, and (3) exposure times of 3, 45, 67, 101, 151, 227, 340, 510 and 765 hours were used. Additional times of 83, 189, 273 hours were used for eggs 48 hours old when initial mortality was high.

Probit anaysis was used to transform sigmoidal dosage mortality curves into straight lines (Bliss, 1935). Variance analysis was used to determine the sources of variation and the effects of the treatment.

Results. Results of this experiment are summarized in Tables 9 to 12 and Figures 4 to 7.

Generally, resistance to cold appeared to increase as the age of the egg increased. Initial mortality occurred after 67 hours with 3 hour old eggs, after 151 hours with 24 hour old eggs, after 227 hours with

Table 5. Effect of continuous exposure to 35.0 C on three hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	32.35	4.5407
120	45.0	84.31	6.0069
120	67.5	100.00	

Treatment F-value 433.06 (F at 1% 4.43) with 4 DF
Between Treatment F-value 1.72 (F at 5% 2.71) with 20 DF

Mean number of hours of exposure at 35 C required to produce 50% and 95% mortality are: 34.45 ± 1.40 and 51.27 ± 3.55 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 6. Effect of continuous exposure to 35.0 C on 24 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	41.66	4.7895
120	45.0	84.26	6.0051
120	67.5	100.00	

Treatment F-value 404.1 (F at 1% level 4.43) with 4 DF
Between Treatment F-value 0.77 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 33.19 ± 3.49 and 48.31 ± 3.34 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 7. Effect of continuous exposure to 35.0 C on 48 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	44.06	4.8516
120	45.0	87.28	6.1407
120	67.5	100.00	

Treatment F-value 805 (F at 1% level 4.43) with 4 DF
Between treatment F-value 0.82 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 32.8 ± 1.33 and 50.03 ± 3.4 respectively. Variance analysis showed that variation in percentage was a function of treatment.

Table 8. Effect of continuous exposure to 35.0 C on 96 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	34.77	4.6093
120	45.0	76.97	5.7388
120	67.5	100.00	

Treatment F-value 426.78 (F at 1% level 4.43) with 4 DF
Between tratment F-value 0.05 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 35.17 ± 1.11 and 54.95 ± 4.14 hours respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 9. Effect of continuous exposure to 5.0 C on three hour old eggs of *Mamestra configurata*.

No. of Individuals tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	1.96	2.92
120	83.0	39.20	4.59
120	101.0	74.00	5.64
120	151.0	100.00	

Treatment F-value 568.84 (F at 1% level 3.85) with 5 DF
Between Treatments F-value 2.44 (F at 5% level 2.6) with 25 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 90.57 ± 2.32 and 118.85 ± 5.87 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 10. Effect of continuous exposure to 5.0 C on 24 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Lenth of Treatment in hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	4.46	3.30
120	189.0	50.14	5.00
120	227.0	82.08	5.91
120	340.0	100.00	

Treatment F-value 733.5 (F at 1% level 3.7) with 7 DF
Between treatments 5.13 (F at 5% level 2.42) with 35 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 193.06 ± 5.09 and 252.93 ± 13.14 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 11. Effect of continuous exposure to 5.0 C on 48 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in Hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	0.00	
120	227.0	11.40	3.700
120	273.0	52.63	5.706
120	340.0	79.82	5.834
120	510.0	100.00	

Treatment F-value 445.7 (F at 1% level 3.51) with 8 DF
Between treatments F-value 2.19 (F at 5% level 2.18) with 40 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 271.64 ± 8.26 and 389.05 ± 17.82 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 12. Effect of continuous exposure to 5.0 C on 96 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in Hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	4.75	3.3354
120	227.0	9.09	3.6654
120	340.0	53.20	5.0803
120	510.0	83.81	5.9463
120	765.0	100.00	

Treatment F-value 811.8 (F at 1% level 3.51) with 8 DF
Between treatments F-value 1.04 (F at 5% level 2.18) with 40 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 337.29 ± 17.52 and 633.87 ± 55.77 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

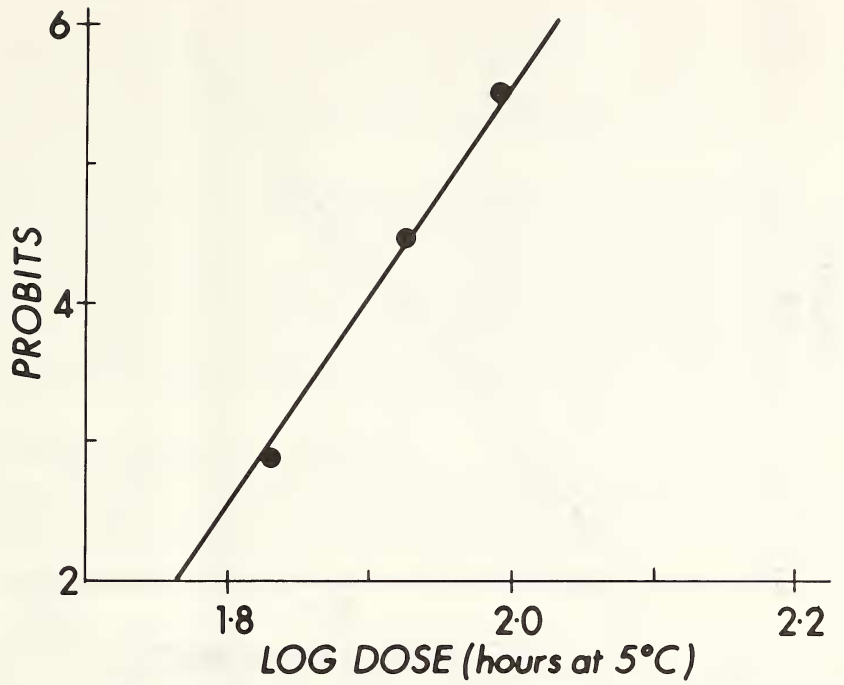

Figure 4. Probit regression line showing the effects of various dosages of 5.0 C on 3 hour old eggs of *Mamestra configurata*.

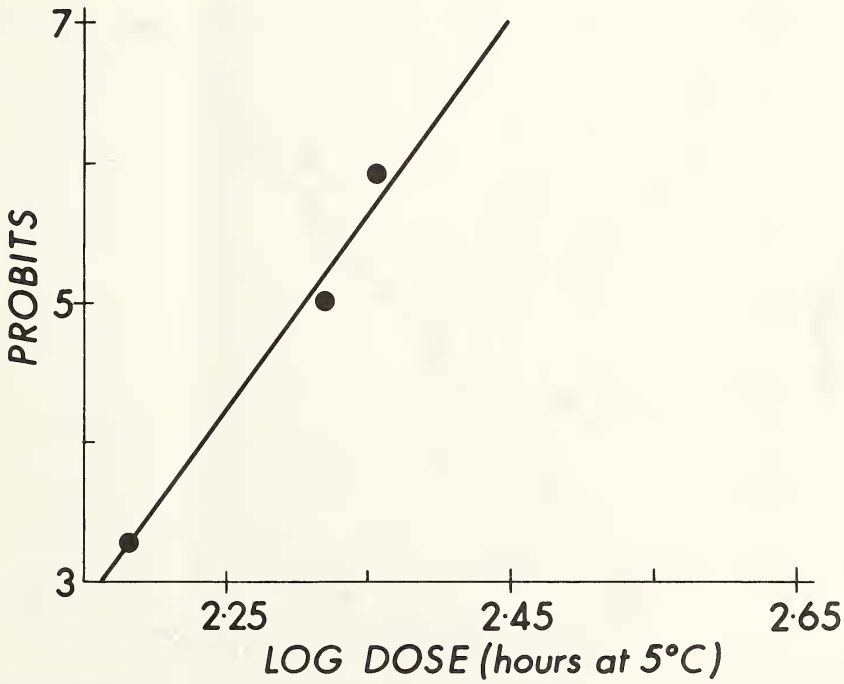

Figure 5. Probit regression line showing the effects of various dosages of 5.0 C on 24 old eggs of *Mamestra configurata*.

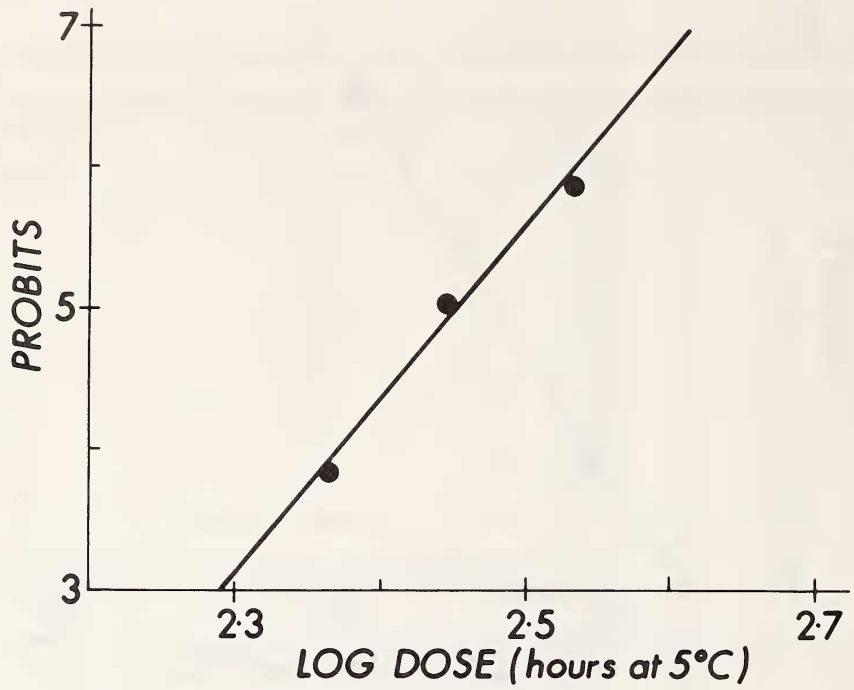

Figure 6. Probit regression line, showing the effects of various dosages of 5.0 C on 48 hour old eggs of *Mamestra configurata*.

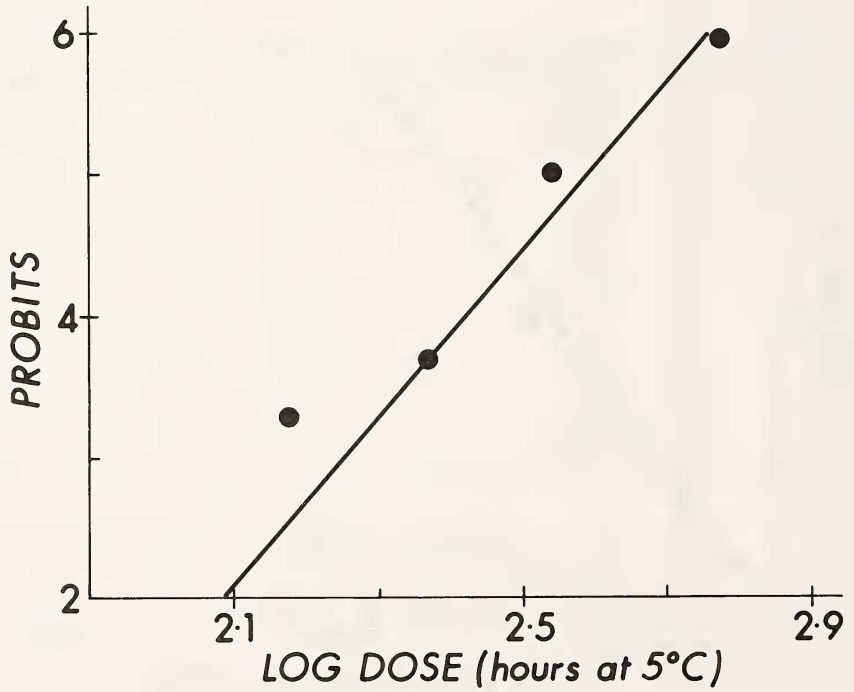

Figure 7. Probit regression line, showing the effects of various dosages of 5.0 C on 96 hour old eggs of *Mamestra configurata*.

48 hour old eggs and after 151 hours with 96 hour old eggs. However, after 227 hours the 48 hour old eggs suffered 11.4% mortality while, after time period, the 96 hour old eggs had only 9.1% mortality. The mortality difference is even greater after 340 hours exposure with 79.8% and 53.2% respectively for the 48 hour and 96 hour old eggs. Probably, there is a developmental age where exposure to 5.0 C is more critical than at other stages.

The increased resistance to cold is better illustrated when LD 50's and LD 95's are compared. Eggs 3 hours old had an LD 50 and an LD 95 of respectively 90.57 ± 2.32 hours and 118.85 ± 5.87 hours. These values for 24 hour old eggs were respectively 193.06 ± 5.09 hours and 252.93 ± 13.14 hours. Eggs aged 48 hours and 96 hours accrued 50% mortality after 271.64 ± 8.26 hours and 337.29 ± 17.52 hours and 95% mortality after 389.05 ± 17.82 hours and 633.87 ± 55.77 hours.

The F-values between error and treatment were highly significant (Tables 9–12), but variance between treatments was significant only for the 24 hour group.

Effects of alternating temperature on development

Alternating temperatures are used in biological temperature research to determine effects that cannot be ascertained using constant temperature alone. For example, under alternating temperatures, eggs of *Oncopeltus fasciatus* (Heteroptera) can complete embryogenesis at a mean temperature several degrees lower than the lowest constant temperature at which complete embryogenesis can occur (Lin *et al.* 1954).

During development, organisms are often subjected to extreme temperatures that would be fatal to them if they were maintained over long periods. Knowledge of the effects of alternating temperature on mortality and rate of development aids us in understanding naturally occurring temperatures effects on development.

Two experiments were conducted on eggs of *Mamestra configurata* to determine the effects of varying daily exposures to extreme temperatures on development rate. The first experiment was designed to determine the effects of daily exposure to 35.0 C on rate of development; the second had 5.0 C as the experimental temperature. In both experiments, the alternate temperature used was 20.0 C.

Effects of daily alternation between temperatures of 20.0 C and 35.0 C on eggs of different ages. – The main purpose of this experiment was to determine if eggs of the experimental population could withstand daily exposure to 35.0 C. In Alberta, the ovipositional period of females of *Mamestra configurata* extends from late June to mid-July so that its eggs would rarely be exposed to a temperature of 35.0 C. However, since *Mamestra configurata* is partially bi-voltine (i.e., it lacks either an obligatory or a facultative diapause in some members of its populations), its eggs may be expected to show partial resistance to daily temperatures of 35.0 C.

The other purpose of this experiment was to determine if alternation of temperature influenced development rate. Alternation of a high temperature with a moderate temperature often results in a decrease in the development rate of an insect compared with its performance at a constant temperature equal to the mean of the alternating temperatures (Johnson, 1940).

Methods. Eggs were collected from a culture reared at 20.0 ± 0.5 C and approximately 60% RH, divided into groups of 10 and each group was placed in a 1 mm cap vial.

Four groups of ten individuals were used at each of 13 experimental exposures (from 1 to 22.5 hours daily at 35.0 C; see Table 13 to 16 for details). Eggs of four different ages (3, 24, 48, and 96 hours) were used to determine the effect of age on tolerance to 35.0 C.

Eggs from any one collection period were divided into as many groups of ten as their number allowed, and the resulting groups were subdivided into units of four. Each of these units was then given daily exposure of 35 C. One vial from each collection was left at 20.0 ± 0.5 C to determine fertility.

During exposure, the vials were placed on a platform in a desiccator. A saturated salt solution of NH_4NO_3 was used to produce an RH of appoximately 60% (Winston and Bates, 1960). First exposure to 35.0 ± 0.5 C was made immediately after the eggs had reached the desired age and was repeated at the same time each subsequent day until completion of the experiment. After exposure, the eggs were returned to 20.0 ± 0.5 C for the remainder of the day.

Eggs were observed daily until they reached the black head capsule stage at which time observations were made at two hour intervals. The number hatching and the total length of the development period for each egg was then recorded.

The mean hatching time for each exposure and the mean temperature for each group was determined. This allowed a comparison to be made between mean development time of eggs maintained at constant temperatures and those maintained under alternating temperatures.

Fry and Surber's (1971) experiment on the effects of exposure to 35.0 C and 40% RH on eggs of *Estigmene acrea* was used as a model.

Results. Results of the various treatments are summarized in Tables 13 to 16. In general, daily exposures of one hour did not result in significant change in development time (Daily exposures of 2.9 hours or greater resulted in a significant change in development time.) regardless of the number of exposures.

Table 13. Effect of daily exposure to 35.0 C on development in three hour old eggs of *Mamestra configurata*.

Number of Individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	6.0	132.514±1.63 A*	**
40	1.3	7.8	132.375±2.30 A	**
40	1.7	10.2	130.32 ±1.65	0.005
40	2.2	13.2	129.33 ±2.70	0.001
40	2.9	17.4	126.00 ±2.27	0.001
40	3.7	20.4	124.82 ±1.89	0.001
40	4.8	24.0	123.4 ±0.45 B	0.001
40	6.2	31.0	123.15 ±2.64 B	0.001
40	8.0	40.0	122.52 ±2.82	0.001
40	10.4	52.0	121.33 ±2.44	0.001

Treatment F-value 114.08 (F at 1% level 2.32) with 9 DF

*means followed by the same letter (A or B) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-tests. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Table 14. Effects of daily exposure to 35.0 C on development in 24 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	5.0	130.51 ± 1.88	**
40	1.3	6.0	130.16 ± 2.15	0.050
40	1.7	7.0	128.43 ± 2.06	0.001
40	2.2	11.0	127.51 ± 1.59	0.001
40	2.9	14.5	125.12 ± 1.75	0.001
40	3.7	15.0	123.92 ± 1.58	0.001
40	4.8	16.0	121.55 ± 2.17 A*	0.001
40	6.2	24.8	121.31 ± 1.95 A	0.001
40	8.0	32.0	120.14 ± 1.63	0.001
40	10.4	40.8	119.33 ± 2.00	0.001
40	13.5	54.0	117.82 ± 1.90	0.001

Treatment F-value 174.89 (F at 1% level 2.32) with 10 DF

*means followed by the same letter (A) are not significantly different (based on Duncan's New Multiple Range Test).

**not significant at the 5% level using T-tests. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Duncan's New Multiple Range Test was used to determine if individual treatments within each experimental group varied significantly from each other. The difference between exposures of one hour and 1.3 hour daily to 35.0 C was not significant in the 3 hour old groups. Non-significant differences were shown also between daily exposures to 4.8 and 6.2 hours for both the 3 hour and 24 hour old groups. Eggs 48 hours old showed no significant difference in development time for daily treatments of 2.9, 3.7, and 4.8 hours, nor between treatments of 4.8 and 6.2 hours and 1.7 and 2.2 hours. Eggs 96 hours old showed no significant difference in development time for daily treatments of 1.0, 1.3, 1.7 or 2.2 hours. No significant variation occurred between treatments of 3.7 and 4.8 or 8.0 and 10.4 hours.

Variance analysis was also used to determine if the variation noted in development times was due to treatment. The resulting values showed that the treatments were highly significant in this.

A comparison between development times observed under constant temperature and under equivalent alternating temperatures showed that development at constant temperatures of 22.5 and 25.0 C occurred more rapidly than at an equivalent temperature produced by daily alternation between 35.0 C and 20.0 C but more slowly at a constant temperature of 20.0 C (Table 17).

Our results were difficult to reconcile with those of Fry and Surber (1971). A single exposure to 35.0 C and 40% RH for 20 hours, resulted in only a 1.6% hatch of salt marsh caterpillar , *Estimene acrea*, eggs whereas all eggs of *Mamestra configurata* hatched that were given a similar exposure to 35.0 C and 60% RH for 22.8 hours. However, three exposures of 16 hours to 35.0 C and 40% RH resulted in 65.7% hatch for salt marsh caterpillar eggs while three similar exposures of 17.5 hours to 35.0 C and 60% RH resulted in only 27.5% hatch for *Mamestra configurata* eggs.

Table 15. Effects of daily exposure to 35.0 C on development of 48 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	4.0	129.94 ± 1.39	**
40	1.3	4.8	129.00 ± 1.63	**
40	1.7	5.6	128.32 ± 1.80 A*	0.05
40	2.2	8.8	128.15 ± 1.74 A	0.05
40	2.9	11.6	126.06 ± 1.64 B	0.001
40	3.7	12.0	125.78 ± 1.62 B	0.001
40	4.8	19.2	125.5 ± 1.54 B C	0.001
40	6.2	23.09	124.49 ± 1.28 C	0.001
40	8.0	28.05	124.05 ± 1.37	0.001
40	10.4	34.7	123.53 ± 1.43	0.001
40	13.5	42.5	122.0 ± 1.30	0.001
40	17.5	51.5	119.27 ± 1.35	0.001

Treatment F-value 105.36 (F at 1% level 2.32) with 11 DF

*means followed by the same letter (A,B,C) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-test. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Effects of daily alternation between temperatures of 5.0 C and 20.0 C on eggs of different ages. – In the province of Alberta, *Mamestra configurata* has been recorded from almost all rape growing areas, a territory extending from south of Lethbridge to north of Keg River, a distance of about 966 km (Philip, pers comm.). Over much of this range, temperatures during the ovipositional period (June to July) could fall to 5.0 C or lower (i.e. below the developmental-hatching threshold, 8.5 C) for short periods (Canadian Department of Transport Meteorological Records, 1971–1974). The primary purpose of this experiment was to determine the effects of a varying exposure to 5.0 C on development time of eggs. A secondary purpose was to determine if alternation of temperatures would produce an acceleration in development over those of eggs maintained at a constant equivalent temperature.

Methods. Methods and materials used in this experiment were identical to those of the previous one except that (1) daily exposure was to 5 C, (2) the saturated salt solution used to maintain 60% RH was $Na_2Cr_2O_7.H_2O$, and (3) 25 rather than ten individuals were used in experiments involving three hour old eggs.

Results. The effects of the various treatments are summarized in Tables 18 to 21.

T-tests were used to determine the significance of the effect oftreatment on development time. In all cases, the treatments produced a significant delay in development as compared with that of controls. Variance analysis was used to determine if the difference noted in development times was a function of treatment. In all cases, the difference noted between development times was highly significant at the 1% confidence level.

Duncan's New Multiple Range Test was used to determine if the individual treatments produced a significant difference in development times within individual test groups. In all cases, this test showed that the treatments differed at the 5% confidence level.

When the rates of development of eggs under constant temperature and under its alternate temperature equivalent were compared, those under the alternating temperatures developed more rapidly (Table 22).

Table 16. Effects on daily exposure to 35.0 C on development of 96 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	2.0	132.78 ±1.10A*	**
40	1.3	2.4	132.75 ±1.32A	**
40	1.7	3.4	132.58 ±1.06A	**
40	2.2	4.4	132.72 ±1.84A	**
40	2.9	5.8	132.058±1.87	0.050
40	3.7	6.0	131.62 ±1.82B	0.050
40	4.8	9.6	131.44 ±1.62B	0.001
40	6.2	12.4	130.91 ±1.66	0.001
40	8.0	16.0	130.00 ±1.61C	0.001
40	10.4	18.96	129.74 ±1.84C	0.001
40	13.5	21.29	128.56 ±1.40	0.001
40	17.5	29.89	127.79 ±1.53	0.001
40	22.5	28.89	126.39 ±1.41	0.001

Treatment F-value 56.39 (F at 1% level 2.32) with 12 DF

*means followed by the same letter (A,B,C) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-tests.

Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Table 17. Comparison of development rate in hours and in hour-degrees at constant temperature and at an equivalent alternating temperature (35.0 and 20.0 C) of eggs of *Mamestra configurata*.

Temperature C°	Development time in hours	
	Constant	Alternating
20.0	135.14 (2703)*	132.16 (2643)
22.5	118.8 (2673)	121.55 (2735)
25.0	100.92 (2523)	119.33 (2983)

*Numbers in brackets are equivalent development rates in hour-degrees.

Table 18. Effects of daily exposure to 5.0 C on development in three hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
100	1.0	6.0	137.54 ± 1.99	0.001**
100	1.3	7.8	138.76 ± 1.84	0.001
100	1.7	10.2	142.08 ± 2.11	0.001
100	2.2	13.2	141.12 ± 1.74	0.001
100	2.9	17.4	142.31 ± 1.83	0.001
100	3.7	25.9	156.51 ± 2.00	0.001
100	4.8	33.6	163.91 ± 1.34	0.001
100	6.2	49.6	180.79 ± 1.57	0.001
100	8.0	64.0	194.76 ± 1.74	0.001
100	10.4	102.5	233.92 ± 1.65	0.001
100	13.5	162.0	289.93 ± 2.11	0.001
100	17.5	332.5	454.20 ± 1.78	0.001

Treatment F-value 550 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development times between treatments was analysed by variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 19. Effects of daily exposure to 5.0 C on development in 24 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	5.0	135.45 ± 0.997	0.001**
40	1.3	6.5	138.50 ± 1.66	0.001
40	1.7	8.5	140.29 ± 1.78	0.001
40	22.2	11.0	141.16 ± 1.61	0.001
40	2.9	14.5	145.83 ± 1.54	0.001
40	3.7	22.2	151.25 ± 2.81	0.001
40	4.8	28.2	160.96 ± 1.35	0.001
40	6.2	37.2	173.07 ± 1.73	0.001
40	8.0	56.0	183.61 ± 1.74	0.001
40	10.4	93.6	230.69 ± 1.76	0.001
40	13.5	136.0	258.5 ± 1.34	0.001
40	17.5	262.5	387.22 ± 1.53	0.001

(continued on page 283)

Table 19. (Continued)

Treatment F-value 63,708 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development time between treatments was analyzed using variance and found to be highly significant and, almost completely, a function of treatment.

Table 20. Effects of daily exposure to 5.0 C on development in 48 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	4.0	138.95 ± 1.90	0.001**
40	1.3	5.2	140.38 ± 1.50	0.001
40	1.7	6.8	142.95 ± 2.01	0.001
40	2.2	8.8	144.82 ± 1.57	0.001
40	2.9	14.5	149.78 ± 1.64	0.001
40	3.7	18.5	155.19 ± 1.91	0.001
40	4.8	24.0	159.66 ± 1.49	0.001
40	6.2	31.0	165.94 ± 1.82	0.001
40	8.0	40.0	176.03 ± 1.46	0.001
40	10.4	62.4	194.72 ± 1.73	0.001
40	13.5	108.0	236.61 ± 1.84	0.001
40	17.5	210.0	339.41 ± 1.52	0.001

Treatment F-value 39,499 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development time between treatments was analyzed using variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 21. Effects of daily exposure to 5.0 C on development of 96 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	2,0	133.83 ± 1.68	0.001**
40	1.3	2.6	135.91 ± 1.74	0.001
40	1.7	2.4	137.03 ± 1.67 A*	0.001
40	2.2	4.4	137.18 ± 1.31 A	0.001
40	2.9	5.6	138.67 ± 1.63	0.001
40	3.7	7.6	140.43 ± 2.71	0.001
40	4.8	9.6	141.84 ± 1.11	0.001
40	6.2	12.4	145.20 ± 1.95	0.001
40	8.0	24.0	156.65 ± 1.81	0.001
40	10.4	31.2	162.17 ± 1.81	0.001
40	13.5	54.0	184.94 ± 1.72	0.001
40	17.5	87.5	219.37 ± 1.66	0.001
40	22.5	308.5	435.33 ± 1.91	0.001

Treatment F-value 78,120 (F at 1% level 2.18) with 12 DF

*means followed by the same letter (A) are not significantly different based on Duncan's New Multiple Range Test.

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development times between treatments was analysed using variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 22. Comparison of development rate in hours and in hour degrees at constant temperature and at an equivalent alternating temperature (5 and 20 C) of eggs of *Mamestra configurata*.

Temperature C°	Development time in hours Constant	Alternating
17.5	220.71 (3862)*	156.5 (2739)
15.0	252.32 (3785)	194.76 (2921)
12.5	462.65 (5783)	387.22 (4840)

*Numbers in brackets are equivalent development rates in hour-degrees.

DISCUSSION AND CONCLUSIONS

Temperature thresholds for embryogenesis

Study of temperature effects on organisms began when Reamur (1735, see Belehradek, 1930) recognized that a relationship exists between temperature and the activity of an animal. Since the, these relationships have been examined by numerous authors and reviewed by Crozier (1926), Belehradek (1930), Uvarov (1931), Janisch (1932), Howe (1967), Bursell (1974) and several others. The results of these studies led to the development of the concept of various temperature thresholds for developmental stages.

These are two principal types of temperature threshold; low temperature thresholds involving temperatures too low for certain developmental processes to be completed, and high temperature thresholds which consider temperatures too high for normal development. Determination of these thresholds, in embryogenesis, has been made primarily of the first type, probably because of the larger temperature coefficients existing between the various thresholds at lower temperatures.

Presently, four low temperature thresholds are recognized as affecting embryogenesis. Peairs (1927) defined the *developmental thresold* as "the temperature at which, on the descending scale, development ceases, and at which, on the ascending scale development is initiated". Johnson (1940) introduced the *hatching threshold* and the *developmental-hatching threshold* which are respectively, the lowest temperature at which hatching of a fully developed larva can occur, and the lowest temperature at which complete development from fertilization to eclosion can occur. The *hatching-survival threshold* was suggested by Hodson and Al Rawy (1956) and they chose Allee *et al.*'s (1949) definition of the "lowest temperature at which a given stage in the life history can be carried through to completion" for a definition.

The only high temperature threshold recognized for embryogenesis is the high temperature equivalent of the developmental-hatching threshold. It has also been suggested that there exists a high temperature threshold equivalent of the developmental threshold, but Uvarov (1931) questioned whether this temperature is distinct from the upper lethal temperature. He further stated that if there was an appreciable difference in temperature between the upper lethal point and the upper developmental threshold, then there should be a quiescent stage similar to the quiescence observed at temperatures below the developmental threshold but above the lower lethal point. This stage, referred to as *heat stupor*, has been recognized in relation to activity but, as yet has not been described for development. Theoretically, this stage could exist, although the range between it and the upper lethal temperature may be so restricted that its discovery will be of limited practical value.

The concept of the developmental threshold of Peairs (1927), has been given numerous names by various authors in attempts to convey with greater clarity the process that occurs at that particular temperature. It has been called "the critical point", "physiological zero" and "the minimum effective temperature" (Uvarov, 1931). More recent authors (e.g. Lin *et al.*, 1954) have chosen to ignore the original definition of this threshold and have used instead Johnson's (1940) developmental-hatching threshold definition as if it were synonymous. The developmental threshold is seldom determined analytically, but is generally arrived at by extrapolation from temperature and rate of development curves. This method assumes that the effects of temperature on duration of embryogenesis can best be represented, mathematically, by a hyperbolic function (Sanderson and Peairs, 1914). This function, when transformed into its reciprocal, produces a straight line. This line is often called the "velocity line", and represents the effects of temperature on rate of development. When plotted on a graph, the point

where the velocity line intercepts the temperature axis is the hypothetical zero of the hyperbola or the developmental threshold. This method is used extensively to derive the developmental threshold; for example it is 11.5 C for the corn earworm, *Heliothis zea* (Boddie), (Luckmann, 1963) and 11.0 C for the European corn borer *Ostrinia nubilalis* (Hubner) (Matteson and Decker, 1965).

The difficulty in using a straight line to describe rate of development was first pointed out by Krogh (1914) and later by Shelford (1927) and Peairs (1927). Peairs noted that the development rate deviated from a straight line near the extremes of the temperature range. Thus, thresholds determined using this method were higher than the actual threshold.

Johnson (1940) emphasized the need for determining thresholds empirically and the necessity of recognizing different thresholds for various stages of embryogenesis. He suggested that because there are distinct stages in embryogenesis, there should also be equally distinct temperature thresholds for development of these stages. He suggested that both hatching and developmental hatching thresholds be used. However, with the exception of a study on eggs of the milkweed bug *Oncopeltus fasciatus* (Dallas) (which showed them to hatch at a temperature 2.0 C lower than their developmental-hatching threshold if 90% of the previous embryonic development occurred at 20.0 C (Lin *et al.*, 1954)) most researchers have chosen to disregard both the hatching and the development-hatching thresholds.

The hatching survivial threshold of Hodson and Al Rawy (1956) has also been ignored by recent workers, probably because of the extensive amount of time required for rearing immatures through to adulthood.

The *upper temperature developmental limit* can be considered to be the upper equivalent of the developmental-hatching threshold or the highest temperature at which complete development and eclosion can occur. This upper threshold has been described in representative species of many orders of insects, e.g. (Collembola) *Onychiurus furciferus* (Borner) (Choudhuri, 1960); (Hemiptera) (*Geocoris atricolour* Montd. (Dunbar and Bacon, 1927); (Diptera) *Phormia regina* Meig. (Melvin, 1934); (Coleopera) *Epilachna corrupta* Mulsant (Pyenson and Sweetman, 1931); and (Lepidoptera) *Telea polyphemus* Cramer (Ludwick and Anderson, 1942). Bursell (1974) listed the upper limit for various insect species, the highest, 40.0 C , being recorded for *Ptinus tectus* Boield; the lowest, 28.0 C, for *Tribolium confusum* (Herbst), both Coleoptera.

The various temperature thresholds demonstrated for embryogenesis in eggs of *Mamestra configurata* show that these are well adapted to Alberta climatic conditions occurring at the time of oviposition. Some development occurs at temperatures as low as 2.0 C and fully developed eggs can hatch at temperatures as low as 5.0 C (3.5 C below the developmental-hatching threshold). Eggs can develop completely and hatch at temperatures ranging from 8.5 C to 30.0 C, temperatures similar to those recorded by Bailey (1976) for eggs of this insect. However, mortality at the developmental-hatching threshold (8.5 C) is high (77.8%). Normal temperatures (mean, maximum and minimum) for the ovipositional period rarely fall outside this developmental range (Department of Transport Meteorological Records).

Similar high mortality at the development-hatching threshold has been demonstrated for eggs of *Oncopeltus fasciatus* by Richards and Suannaksa (1962). It is probable that the larvae that hatched would not have reached maturity. Their hatching behaviour showed the same anomalies as those reported by Lin *et al.* (1954) for nymphs of *Oncopeltus fasciatus*. They found that even if these nymphs were tranferred to ideal conditions, very few reached maturity. Larvae hatching under these conditions appear debilitated and have difficulty moving effectively. It is possible that these larvae have internal structural defects that result in early death.

The upper developmental-hatching threshold for eggs of *Mamestra configurata* recorded here (between 30.0 C and 31.5 C) is comparable to the 32.0 C value given by Bailey (1976) for eggs of this

species and resembles that of eggs of the armyworm, *Pseudaletia unipuncta* (Howe) (Guppy, 1969). He found that the rate of development for eggs of this species began to decrease when temperature was increased above 29.0 C. Eggs of *Mamestra configurata* probably follow a smilar course of development. The lack of data supporting this belief probably arises from experimental error. Sample sizes (50 individuals) may have been too small to reveal the small percentage of individuals that might have hatched at temperatures above 30.0 C. Also, the interval between 30.0 C and the next temperature (31.5 C) might have been too large. Mortality in insects increases rapidly as temperature increases above their optimum temperatures (Stinner *et al.* 1974). Even if complete development is curtailed by temperatures in excess of 30.0 C, the occurrence of these temperatures in Western Canada during the incubation period is rare and would have little effect on development.

Effects of constant temperature and relative humidity on embryogenesis

Research conducted on the effects of temperature on insect embryogenesis can be broadly classed into two groups. The first treats the effects of constant temperature (often applied at different relative humidities); the second, the effects of alternating or varying temperatures on embryonic development. This subject has been reviewed by Sanderson (1910), Uvarov (1931), Janisch (1932), Howe (1967) and Bursell (1974) . The effects of relative humidity have been reviewed by Buxton (1932) and Ludwick (1945).

One of the principal reasons that the effects of constant temperature on insect development are studied is the hope that the resulting developmental curves can be used to predict insect development in the field. Numerous attempts have been made to derive a general mathematical function or equation that describes the relationship between temperature and development in insects. These attempts have been reviewed by Crozier (1926), Uvarov (1931), Janisch (1932), Davidson (1944), and Howe (1967). The more widely used of these concepts are: day-degrees; thermal summation and summation of development units.

Improper use of these concepts often leads to grossly inaccurate results. This occurs when fluctuating temperatures are assessed in terms of a simple average rather than weighted according to the effects of each individual temperature on development (Bursell, 1974). The inaccuracy of these concepts arises from the assumption that the best way to represent mathematically the effect of temperature on rate of development, is through use of a straight line. Near the extremes of the temperature range for a species, the rate of development deviates from a simple linear relationship. At the lower extreme, the rate of development declines more slowly; at the upper extreme, more rapidly than would be expected from a strictly linear relationship. The resulting temperature and rate of development curve is thus closer to being sigmoidal than linear. However, when the temperature range between the maximum rate of development and the upper lethal limit is slight, the resulting curve is J-shaped (Howe, 1967).

Relative humidity can apparently have no effect on insect embryogenesis; or it can cause changes in development time, and influence mortality rates and developmental thresholds. These effects and others on invertebrates have been reviewed by Buxton (1932) and Ludwick (1945).

The rate of embryogenesis in eggs of *Mamestra configurata* showed a strong linear relationship with temperature over the range of temperatures used in this experiment. Deviation from this relationship occurred only at temperatures of 10.0 C and lower. Complete development and hatching occurred at temperatures ranging from 8.5 C to 30.0 C.

Low humidity retarded development regardless of temperature. It is possible that eggs of *Mamestra configurata* normally absorb from the atmosphere at least a portion of the water used during development. Extremely low humidity would inhibit this absorption and force development to rely upon already present reserves, thus slowing down rate of development.

Lower temperatures prolonged exposure to low humidities and resulted in increased mortality. Possible causes for this are (1) death due to desiccation as the eggs had insufficient water to complete development, (2) weakening of larvae through water loss, making the act of hatching more difficult, and (3) hardening of the chorion caused by desiccation, inhibiting hatching, or (4) by a combination of these factors.

The fastest rate of development always occurred at 98% RH followed by 60% RH and 0% RH. This suggests that eggs of *Mamestra configurata* absorb water during development and that water may become the limiting factor during some part of embryogenesis. Water absorption would be faclitated most in high humidity, and would decrease as humidity declines. It is unfortunate that we failed to monitor micro-climatic conditions within blossoming rape fields since such data would have faclitated speculation of this kind.

Effects of exposure to constant temperature and relative humidities of 0%, 60% and 90% on developmental rate. – In general, low relative humidity retards rate of development in insect eggs. We have shown this to be true too for eggs of *Mamestra configurata*. Regardless of the temperature used, hatching always occurred first at 98% RH followed by 60% and 0%. Relative humidity appeared to be more important in the lower temperature range (15.0 to 8.5 C). At 0% RH, hatching was inhibited at temperatures below 15.0 C. At the developmental-hatching threshold (8.5 C) hatching occurred only at 98% RH.

Bailey (1976) reared eggs of *Mamestra configurata* at 75% RH and at temperatures of from 6.0 to 36.0 C and found the time for completion of embryogenesis and hatching to decrease from 28 days at 8.0 C to 3 days at 28.0 and 32.0 C. These figures are similar to those recorded here: 36.6 days at 8.5 C and 98% RH, 3.2 days at 30.0 C and 98% and 3.3 days at 30.0 C and 60% RH (Table 4). These results agree with those reported for other Lepidoptera (Ludwick and Anderson, 1942).

Evidence from our experiments to suggest that both mechanical and physiological barriers retard and reduce hatching is that the number of individuals first to eclose at each of the humidities used remained relatively constant regardless of temperature. Differences of eight to ten hours occurred in eggs exposed to RH's of 0% and 98%. This evidence also suggests that the larvae were weakened and thus took longer to hatch. There is also evidence suggesting a physiological delay. Eggs exposed to 0% RH always required a longer time to develop brown pigmentation than did those exposed to higher humidities. This suggests that early stages of development are impaired by lack of access to atmospheric moisture. In many insects, development is enhanced by absorption of atmospheric moisture through a hydropyle (Wigglesworth, 1972). Although examination of eggs of *Mamestra configurata* failed to locate a similar structure, the numerous aeropyles present in the chorion could act in a similar capacity (Jones, 1979).

The experiments we conducted were not designed to determine the mechanism by which humidity affects development. Experiments using a greater range of humidities and tests of egg shell tensile strength would aid in determining which of physiological or mechanical barriers have the greater effect on mortality and rate of development.

Effects of constant exposure to a temperature of 35.0 C on development of eggs of different ages. – Constant exposure of eggs to 35.0 C produced approximately 50% mortality after 37 hours and 95% mortality after 20 hours regardless of egg age. (Tables 5–8). Comparison of the 50% and 95% mortality times of eggs of different ages demonstrated that older eggs had slightly more tolerance than their younger counterparts. However, the difference was slight and only much larger sample sizes and a greater number of exposures would demonstrate if the difference is significant.

Sensitivity to high temperature decreased in eggs of the silkworm *Bombyx mori* L., after meiosis but before syngamy (Ostryakova-Varshaver, 1958). The exact cause of death in these eggs at high temperatures was unknown. Denaturing of proteins, an upset in the balance of one or more metabolic

processes leading to accumulation of some toxic product of metabolism more quickly than it can be removed, desiccation, or starvation have all been suggested as contributing to heat death (Bursell 1974). It is possible that older eggs of *Mamestra configurata*, i.e. those 24, 48, and 96 hour old, might have shown greater resistance to heat if they had been kept at 30.0 C prior to testing them at 35.0 C. For example, eggs of *Drosophila* spp., show considerable variation in survival time depending upon the temperature at which the flies were reared. Rearing at 25.0 C more than doubled their survival time at 33.5 C compared with that of counterparts reared at 15.0 C (Chapman, 1971).

Two types of acclimation have been demonstrated in insects: a longlasting "developmental" acclimation and a transitory "physiological" one (Bursell, 1974). The first of these depends upon the temperature at which the insect was raised prior to treatment. Insects raised at higher temperature require a longer exposure to a particular high temperature to produce mortality than do their counterparts raised at a lower temperature. This acclimation appears to be permanent and is not affected by exposure to lower temperatures. Physiological acclimation, is readly reversible, its effectiveness being a function of both the temperature and length of exposure experienced prior to exposure to the experimental temperature (Bursell, 1974). For example, in one insect, the chalcid parasite *Dahlbominus fuscipennis* (Zett.) Baldwin and Riodin (1956) (*in* Bursell, 1974) found that the greatest amount of acclimation occurred after two hours exposure and declined to insignificant levels in the next 12 hours.

Effects of constant exposure to a temperature of 5.0 C on development of eggs of different ages. – Constant exposure of eggs of *Mamestra configurata* to 5.0 C had varying results (Tables 9–12). Resistance to cold increased with increasing age, suggesting that early stages of embryogenesis are more sensitive to low temperature. Thus, such stages may require daily exposure to favourable temperature before they can complete development (Lin *et al.*, 1954). Two day old eggs of the cabbage looper, *Trichoplusia ni* exposed to 11.0 C showed increased mortality compared to that of one or three day old eggs (Kishabo and Henneberry, 1966).

Death of embryos at low tempeature may result from structural abnomality. For example, some embryos of *Bombyx mori*, stored at low temperatures, showed the following abnormalities: the amniotic cavity was larger than normal and was broken in some individuals. Others showed incomplete dorsal closure, resulting in parts of the alimentary canal being left outside the body (Totani, 1960). It thus appears that constant exposure to low temperature can disrupt metabolism and subsequent development of the embryo.

Another cause of death caused by continuous exposure to low temperature may be a lack of sufficient food reserves to allow for complete development once the eggs are returned to a favourable temperature (Richards, 1964). This does not appear to be the cause of death for three hour old eggs of *Mamestra configurata* since none of these showed any deposition of pigment (a sign that they had not developed significantly at the end of treatment). As in the previous experiment different results would have occurred if the eggs had been pre-conditioned prior to exposure to the experimental temperature.

Effects of alternating temperature on development

Research on the effects of alternating temperature on insect embryogenesis are of the following types: (1) a low temperature is alternated with a medial temperature (medial temperatures are a range of temperatures for an insect species, where the rate of development most closely approaches a linear relationship with temperature), (2) a high is alternated with a medial, (3) two medial temperatures are alternated with each other, or (4) a temperature series based on field conditions is used to simulate natural conditions.

These effects have been reviewed by Uvarov (1931), Howe (1967), Wigglesworth (1972) and others.

In general, such treatment can (1) accelerate development rate, (2) decrease development rate, (3) influence the developmental-hatching threshold, (4) influence mortality, or (5) have no effects.

Exposure to alternating temperatures appeared to either increase or decrease development rate in eggs of *Mamestra configurata* depending on the situation. Alternation between 5.0 C and 20.0 C apparently accelerated development compared with that of eggs experiencing an equivalent constant temperature whereas alternation between 20.0 C and 35.0 C seemed to decrease development rate.

Effect of daily alternation between temperatures of 20.0 C and 35.0 C on eggs of different ages. – Eggs of *Mamestra configurata* demonstrated an increasing tolerance to longer daily exposures to 35 0 C as they matured (Tables 13–16). Eggs two days old at the beginning of the treatments withstood longer daily exposures than did younger eggs. However, this does not mean that they showed a greater overall resistance to temperatures of 35.0 C. When the total time spent at 35.0 C is compared, it shows that regardless of age no eggs hatched from any group exposed to more than 55 hours. This data, combined with that of the experiment on constant exposure to 35.0 C (Tables 5–8) suggest that the effects of 35.0 C may be cumulative. If this is true, it is unlikely that any one stage of embryogenesis is the most susceptible. Rather, it suggests that the whole of metabolism is disrupted, perhaps leading to a build up of toxic materials which, in turn, causes death (Bursell, 1974).

The time required for complete development was greater under alternating than under constant temperature (Table 17). This agrees with similar results recorded for eggs of the Japanese beetle, *Popillia japonica* by Ludwick (1938), for those of *Drosophila melanogaster* Meigen by Ludwick and Cable (1933) and for those of other fruit flies by Messenger and Flitters (1958). The reason for this is the sigmoidal nature of the temprature and rate of development curves. Above the optimum temperature (30.0 C for eggs of *Mamestra configurata*), rate of development begins to decline, this decline increasing rapidly as temperature increases. Thus, the actual rate of development at 35.0 C is probably similar to that occurring at 30.0 C or lower. This means that the time spent at 35.0 C is equivalant to an identical time spent at 30.0 C and that this should be calculated on this basis rather than on a hypothetical linear relationship supposedly existing between temperature and development curves. If the actual sigmoidal relationship is used, neither a retardation nor acceleration of development would appear to occur.

Eggs of *Mamestra configurata* react similarily to those of the saltmarsh caterpillar, *Estigmene acrea*, when exposed to 35.0 C (Fry and Surber, 1971). This suggests that eggs of *Mamestra configurata* are sufficiently tolerant to survive temperatures found in the south-western United States if the ovipositional period of *Mamestra configurata* there is similar to that of *Estigmene acrea*.

Effects of daily alternation between temperatures of 5.0 C and 20.0 C on eggs of different ages. – The effects of daily exposure to 5.0 C are more applicable to conditions found in Alberta. This experiment showed that eggs of *Mamestra configurata* are well adjusted to Alberta climatic conditions. Temperatures of 5.0 C, when alternated with a favourable temperature (20.0 C), do not have an appreciable effect on mortality (Tables 18–21). The only instance of high mortality was when eggs were exposed to 5.0 C for more than 22 hours daily. In these, hatching occurred only in the 96 hour group (Table 21) even though development to the black head capsule stage occurred in all eggs tested. Failure of these eggs to hatch was probably because the larvae within were debilitated by long exposure to 5.0 C. These results compare favourably with those of Lin *et al.* (1954) who found that as little as one hour per day spent at a favourable temperature allowed complete development of eggs of *Oncopeltus fasciatus*.

Time required for development was shorter under alternating than under constant temperature (Table 22). Similar results have been recorded for eggs of the noctuids *Agrotis orthogonia* and *Chorizagrotis auxiliaris* (Cook, 1927). There are two reasons for this apparent acceleration: (1) some development is taking place at 5.0 C (see Ms p 13), and (2) due to the sigmoidal nature of the temperature-rate of development curve, lower temperatures (5.0 C) contribute less to total development

than do those above the mean (Johnson, 1940).

Evolutionary and practical considerations

It is probable that the species *Mamestra configurata* originated further south and has gradually expanded its range northward. This would explain the existence of the partial second generation which still occurs in Alberta. Eggs of *Mamestra configurata* also show some resistance to temperatures that they are unlikely to experience in Alberta.

Results of this study, hopefully, will be used to remove some of the guesswork in making larval surveys of this insect. Even working with only mean, minimum and maximum temperatures, it will be possible to estimate hatching with some accuracy. Proper timing of the survey will allow for implementation of a more efficient control program. Up until now, control was not usually begun until the larvae had reached at least the fourth instar and caused considerable damage. Control measures directed against earlier instars will result in less damage occurring and in better control.

Further investigation should be conducted to determine if 30.0 C is actually the upper development-hatching threshold. Larvae which survived either constant high or low temperatures during embryogenesis should be reared to adulthood to determine what, if any, effects these treatments have on larvae, pupae, and adults.

The effects of humidity should be studied in greater detail to find out the mechanism or mechanisms by which development is affected. A possible starting point would be to determine if eggs of *Mamestra configurata* absorb moisture and if so to find out whether it is an active or a passive process. Additional field research is necessary to determine the relationships existing between air temperature, relative humidity, and micro-climate in rape fields and the effects of these on embryonic and larval development in *Mamestra configurata*. Predictions based only on general air temperature and relative humidity data may not be as reliable (Bursell, 1974).

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